ART. IV. *BRACHYHYOPS*, A NEW BUNODONT ARTIODACTYL FROM BEAVER DIVIDE, WYOMING

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Text-figures 1-5

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INTRODUCTION

The Carnegie Museum palæontological expedition of 1934, under the leadership of Mr. J. LeRoy Kay, discovered a rather well preserved skull of a bunodont artiodactyl on Beaver Divide, Wyoming. The specimen was found in association with a primitive type of oreodont, in the uppermost portion of the Uinta formation at the locality mentioned, at a situation very close to the boundary between the Uinta and the overlying Oligocene beds.

Through the kindness of Dr. A. Avinoff, Director of the Carnegie Museum, and of Mr. J. LeRoy Kay, of the Department of Vertebrate Palæontology of the same institution, the above mentioned specimen has been given to me for the purposes of study and description. I wish to thank them for the courtesies extended to me in connection with this study.

The illustrations accompanying this description were made by Mr. Sidney Prentice of the Carnegie Museum.

Brachyhyops Colbert[1].

Diagnosis: Of medium size, the skull being of a length comparable to that of the skull of a modern peccary. Dentition $^{3(?)-1-4-3}$; lower dentition unknown. Cheek teeth closely comparable to those of *Chœropotamus*, *Helohyus*, *Achœnodon* and *Parahyus*, being near to the latter in size. Cranium broad, having widely separated parietal crests. Orbit closed posteriorly; situated above the last two molars. Muzzle relatively short, so that the postorbital length exceeds somewhat the preorbital length of the skull. Zygomatic arch vertically

[1] βραχυ's—short; νός—hog; ὀψ—aspect.

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expanded behind and below the orbit, somewhat in the manner of the entelodonts. Skull transversely broad, due to the lateral expansion of the arches. Glenoids shallow and broad and relatively low, being about on a level with the occlusal line of the upper cheek teeth. Paroccipital processes short and pterygoids weak. Posterior nares extending to the middle of the upper third molar. Basicranium primitive, the arrangement of the foramina being like that in the dichobunids.

Generic type: Brachyhyops wyomingensis Colbert.

Brachyhyops wyomingensis Colbert.

Colbert, E. H., 1937, Amer. Jour. Sci., XXXIII, pp. 473-474.

Type: Carnegie Mus., no. 12048, a skull, virtually complete; paratypes, none.

Horizon: From the uppermost level of the Uinta formation, immediately beneath the basal Oligocene agglomerate at Beaver Divide.

Locality: One half mile north of Wagon Bed Springs, Wyoming.

Diagnosis: The specific diagnosis is the same as that given for the genus.

FIG. 1. Beaver Divide, near Wagon Bed Springs, Wyoming. The cross shows the position at which *Brachyhyops wyomingensis* was discovered.

DESCRIPTION

The Skull

As was mentioned in the diagnosis, the new genus now under consideration is of medium size, being more or less comparable in this respect to the modern peccary. It is much larger than the primitive Eocene dichobunids, such as *Homacodon*, much smaller than the genus *Achænodon*, and closely comparable in size to the European form, *Chœropotamus*, and, as judged on the basis of the upper teeth, to *Parahyus*, of the Lower Eocene of North America.

As seen from the dorsal side, the skull of *Brachyhyops* is very broad in comparison to its length. The zygomatic arches are widely expanded as in *Chœropotamus*, or as in *Achænodon uintense*, but except for this character the skulls of *Brachyhyops* and this latter form are quite different from each other in their dorsal aspect. In *Achænodon* the zygomatic arch sweeps around in a rather broad, even curve, from the infraorbital foramen to the postglenoid border. In *Brachyhyops* the arch expands laterally from the infraorbital foramen to a point opposite the posterior border of the orbit, and then it continues posteriorly in a straight line parallel to the midline of the skull. At the back the postglenoid border is transverse and its junction with the lateral portion of the zygomatic arch takes the form of a distinct right angle. The heavy postorbital processes of the frontal and the zygomatic are joined to form a strong postorbital bar.

Noteworthy characters of this skull are to be seen in the widely separated temporal crests, and the vertical expansion of the zygomata. Evidently there was a great enlargement of the temporal and masseter muscles in *Brachyhyops*, which resulted in extraordinary developments of the bony attachments for these muscles. In *Chœropotamus*, *Helohyus* and *Achænodon*, the sagittal crest is high, as in many Eocene mammals, but there is no particular vertical expansion of the zygomatic arch. In the entelodonts the jugal is expanded (whether this is entirely an adaptation for an enlarged masseter may be questioned) and the sagittal crest is strong. In many advanced artiodactyls there are separate parietal crests, formed by a primary longitudinal division of the sagittal crest and a subsequent lateral spreading of the two crests away from the median line, due to the expansion of the brain case. In these cases, however, the division of the sagittal crest and the lateral separation to form two parietal crests is an adaptation

either to an increase of the brain itself, or to the secondary development of enlarged sinus cavities. In *Brachyhyops*, a primitive form with a small brain, it would seem as if the development of the parietal crests was an independent response to an enlargement of the temporal muscles, in no way correlated with a needed increase of cranial capacity, a conclusion based on the fact that the crests are narrow and high, not low ridges on an expanded cranium. A low median ridge in the position of the sagittal crest, may be seen on the skull roof between the two parietal crests.

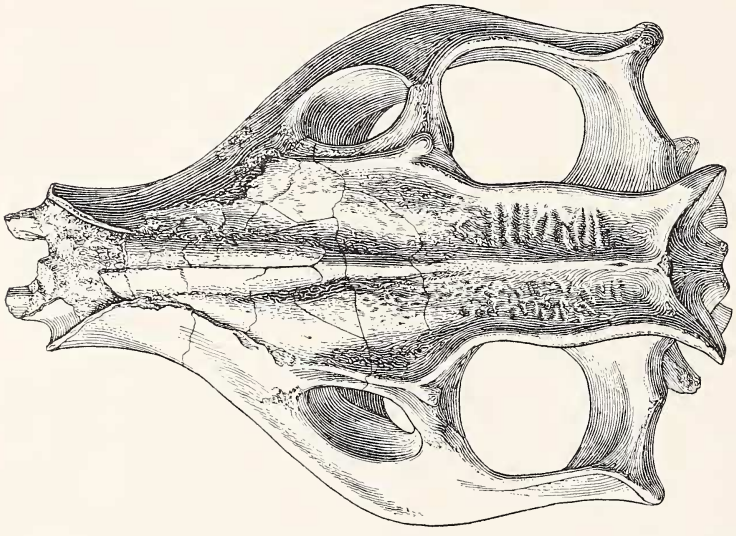

FIG. 2. *Brachyhyops wyomingensis* Colbert. Type skull, Carnegie Mus. No. 12048. Dorsal view, two-fifths natural size.

The frontal and parietal region between the two crests would seem to have been somewhat concave, although crushing has altered this portion of the skull considerably, making it difficult to restore the cranial roof to its original condition. The lambdoidal crest is bowed forward strongly. It might be well to mention in passing that the top of the skull is characterized by a sort of sculptured surface; that is, there are excrescences in the form of low, heavy ridges above the orbits and on the parietals between the parietal crests.

As seen from the side, the appearance of the skull has been greatly altered by crushing, but when the effect of this crushing is disregarded, it may be assumed that the skull was rather low. The orbit is rather

centrally located, that is, it is more or less midway between the front and the back of the skull. The muzzle of *Brachyhyops* is short and the postorbital region is relatively long, in which respects this genus is like the primitive dichobunids, and *Achænodon*. The orbit is closed, as was mentioned above, and the infraorbital foramen is above the third premolar.

The most striking feature about the skull of *Brachyhyops* as seen in a lateral view is the expansion of the malar, as was mentioned above. As in the Entelodontidæ, this expansion is in the jugal beneath and behind the orbit, and it does not extend to the zygomatic process of the squamosal to any pronounced degree. The zygomatic process has a concave depression on its lateral surface, opposite the glenoid.

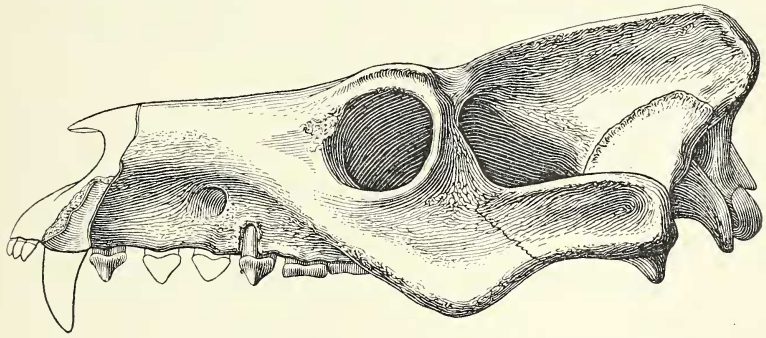

FIG. 3. *Brachyhyops wyomingensis* Colbert. Type skull, Carnegie Mus. No. 12048. Side view, two-fifths natural size.

The external auditory meatus is located between the postglenoid and paroccipital processes and is directed laterally.

The palatal view of the skull of *Brachyhyops*, like the dorsal view, reveals the great breadth of the skull. Due to the expansion of the zygomatic arch, there is a broad area on the ventral side of the jugal, external to the molar teeth and beneath the sphenopalatine foramen, and it continues back, on the ventral side of the jugal and on to the ventral portion of the zygomatic process to merge into the shallow glenoid. The transverse glenoid is extremely shallow and the postglenoid process is transversely broad. The pterygoid processes are of moderate size.

The posterior nares extend to a point opposite the mid-portion of the last molars. The paroccipital processes are short and stout, and di-

rected strongly towards the rear, a character of primitive ungulates. The tubercles of the basioccipital (for the attachment of the rectus capitis ventralis major muscles) are small but well defined.

Turning now to a consideration of the foramina, it is to be noted that the posterior palatine foramina are opposite the anterior border of the second molar. Since the skull is badly crushed, the ethmoid and optic foramina are not discernible, but the foramen rotundum and the foramen lacerum anterius are plainly visible, enclosed in a common vestibule. The foramen ovale is situated just medially to the internal border of the glenoid, while the foramen lacerum medius and the opening for the eustachian canal are behind it and separated from it by a bony ridge. The foramen lacerum posterius is isolated and located opposite and median to the postglenoid process, while the stylomastoid foramen is postero-lateral to the foramen lacerum posterius. The condylar foramen would seem to be single.

This arrangement of the basicranial foramina, described above, is characteristic of a primitive mammal, in that there is little tendency towards fusion or concrescence of the various openings in the cranial floor. In this respect *Brachyhyops* may be compared with other primitive Eocene bunodont artiodactyls, such as *Achænodon*, *Helohyus* and *Cebochœrus*.

It would seem as if the bulla in *Brachyhyops* was either cartilaginous or so fragile (if bony) that it was destroyed, in which respect *Brachyhyops* is similar to other primitive artiodactyls, such as the dichobunids.

In this discussion of the basicranium of *Brachyhyops* it might be well to point out the fact that this genus displays its relationships to the primitive bunodont artiodactyls by reason of the lack of any appreciable compression of the structures on the floor of the brain case. Thus it may be contrasted with the achænodonts and the entolodonts, in which the basicranium is greatly compressed by the backward shift of the glenoids.

The occipital view of the skull of *Brachyhyops* demonstrates again its low, broad character. The condyles are of normal size and development.

The Dentition

The teeth of the specimen under consideration are fragmentary and badly worn, so that unfortunately they are not of much help in a study of this new genus. The last premolar and the last two molars are pres-

ent on the right side of the skull, and the first and last molars are present on the left side. The alveoli of the other cheek teeth and of the left canine are preserved, and thus some deductions as to the dental formula and the arrangement of the cheek teeth are possible.

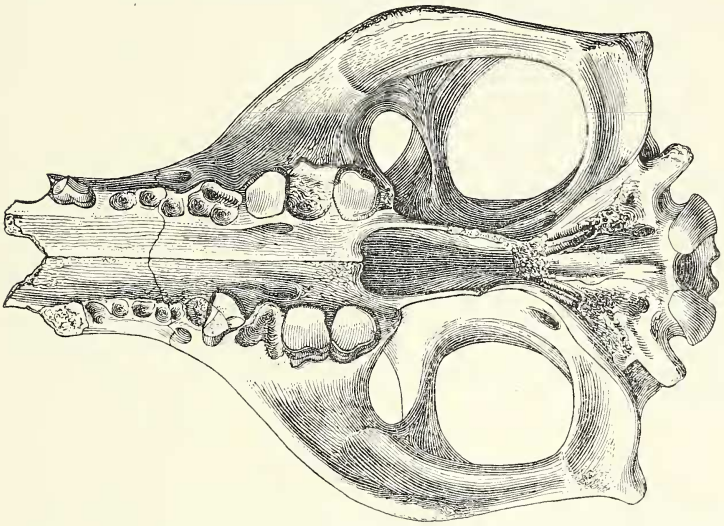

FIG. 4. *Brachyhyops wyomingensis* Colbert. Type skull, Carnegie Mus. No. 12048. Palatal view, two-fifths natural size.

There are four premolars and three molars in *Brachyhyops*. There was seemingly a large canine. There was very probably a full set of incisors, although it is impossible to make a definite statement about these teeth.

The canine, premolars and molars are in a closely set series, without diastemata between them, and in this respect *Brachyhyops* is like *Chœropotamus*, *Achœnodon*, *Helohyus* and other Eocene bunodont artiodactyls. A crown view of the teeth of *Brachyhyops* shows that they are very similar in outline to the teeth of *Chœropotamus* and of *Achœnodon robustus*, as figured by Peterson (1919), except of course that in the latter form the teeth are much larger. The single upper molar of *Parahyus vagus*, as figured by Marsh, also has an outline quite similar to the outline of the second molar in *Brachyhyops*. Marsh identified the tooth that he described as a third upper molar, but this identification may possibly be wrong.

From the alveoli it would seem that the first, second and third pre-

molars in *Brachyhyops* were simple, double rooted teeth, elongated somewhat antero-posteriorly. Probably each tooth consisted of a single cone, laterally compressed, with anterior and posterior keels, the anterior edge being slightly convex and the posterior one slightly concave, with a slight heel or shelf at the back near the base of the tooth. The fourth premolar is a three rooted tooth, the single root being internal. Although much worn, it gives indications of having a large, single outer cone and a smaller inner cone.

The molars are quadrate, and wider than they are long. They were probably quinquetubercular, like the molars of *Chœropotamus* and *Parahyus*, with the protocone, protoconule, paracone, metacone and metaconule comprising the crown of each tooth. The posterior half of the last molar is much reduced, so that the metacone is much smaller than the paracone. The surfaces of the teeth are so greatly worn that it is impossible to make any remarks about the development or the arrangement of the cusps. The third molar shows a slight antero-external cingulum.

Measurements

Brachyhyops wyomingensis

Carnegie Museum no. 12048, skull

Skull	mm.
Length, condyle—front edge of canine	229
Length, condyle—incisors (estimated)	240
Length, preorbital portion of skull (approximate)	105
Length, postorbital portion of skull	135
Width, at glenoids	151
Width, zygomatic arches below orbits	161
Width, palate at first molar	24
Width, occipital condyles	48
Width, frontals at postorbital bar	83
Width, parietals between parietal crests	52
Diameter of orbit (approximate)	35
Depth, jugal beneath postorbital process	45
Dentition	
P^4, length	15
width	15
M^1, length	14
width	17
M^2, length	16
width	20
M^3, length	15
width	18

Comparisons

Now that a description of *Brachyhyops* has been presented, it might be well to compare this new genus with other genera of primitive bunodont artiodactyls for the purpose of determining, if possible, the forms to which it is most closely related. The genera or groups that may be considered in this comparison are as follows:

1. The Dichobunidæ —particularly *Homacodon* and *Wasatchia.*
2. The Chœropotamidæ —both the Helohyids as exemplified by *Helohyus* and the Chœropotamids as typified by *Chœropotamus* and [*Parahyus*].
3. The Cebochœridæ —*Cebochœrus.*
4. The Entelodontidæ —Achænodontinæ and Entelodontinæ.
5. The Tayassuidæ —*Perchœrus.*

The Anthracotheriidæ and the Agriochœriidæ.

1. Dichobunidæ

The Dichobunidæ, being small, primitive, early Eocene artiodactyls are naturally more generalized in many of their characters than is *Brachyhyops.* The common characters in the form now under consideration and these early artiodactyls are the primitive heritage features that might be expected to persist in an upper Eocene genus. Thus the basicranium of *Brachyhyops* is similar to that in *Homacodon* in that it shows the primitive separation of the foramina, the lack of a bony bulla, short, backwardly projecting paroccipital processes and very little anteroposterior compression. In this latter character, however, *Brachyhyops* does show a certain amount of compression, particularly because of the backward migration of the glenoids into a position of close proximity to the auditory region. In most of the cranial and dental characters the dichobunids are much more primitive than is *Brachyhyops* and thus are no more closely related to this genus than to other upper Eocene bunodonts.

2. Chœropotamidæ

There are many resemblances, as well as certain differences, to be seen between *Brachyhyops* and the European genus, *Chœropotamus.*

For this reason it may be well to devote a considerable amount of attention to a detailed comparison between these forms.

Brachyhyops is like *Chœropotamus* in the following ways:

1. Size.
2. The outlines of the cheek teeth.
3. The central position of the orbit above the second and third molars.
4. The shape of the glenoid—a broad, flat articulation merging anteriorly into the lower surface of the zygomatic arch.
5. The transversely broad postglenoid articulation.
6. The low position of the glenoid on a horizontal line with the occlusal surface of the teeth.
7. The short, backwardly projecting paroccipital processes.
8. The probable lack of an ossified bulla.
9. The arrangement of the basicranial foramina.

Brachyhyops differs from *Chœropotamus* as follows:

1. The relatively short, wide skull. In *Chœropotamus* the skull is elongated in the region of the muzzle.
2. The expansion of the zygomatic arch, both laterally and vertically.
3. The closed orbits.
4. The double parietal crests.
5. The broad occiput.
6. The closed dental series, a corollary of the short muzzle.

It is difficult to know just how these resemblances and differences may be evaluated against each other. Should the primitive, basic heritage characters by which the two genera resemble each other be given greater weight than the more specialized habitus characters? It would seem, taking all factors into account, that the heritage characters do give evidence of some degree of relationship between *Brachyhyops* and *Chœropotamus*, and that the specializations in the former genus, such as the expansion of the zygoma, the closed orbits, and the broad cranial roof with its double crests are habitus characters that have been molded over an essentially chœropotamid skull, and that they have been obtained at a relatively late date in the phylogenetic history of the genus.

Now we may consider briefly the resemblances and differences between *Brachyhyops* and *Parahyus*. This latter genus contains two species, *Parahyus vagus*, known from a mandibular ramus, and *Parahyus aberrans*, based on a single upper molar tooth. Both of

these species are from the Wasatch formation of Lower Eocene age. *Parahyus* has usually been referred to the Achænodontidæ (or grouped with *Achænodon*, whatever might be the systematic position of this latter genus) but it may be noted here that Matthew[2] questioned this reference in 1909. It seems to me much more likely that *Parahyus* is a true chœropotamid, because it is closely comparable to *Chœropotamus*, not only in size but also in the shape and structure of the upper and the lower teeth.

Helohyus, also, would seem to be a primitive chœropotamid, as Matthew suggested in 1925[3], and as such is comparable to *Brachyhyops*.

All in all, therefore, there is much reason to think that *Brachyhyops* is closely comparable to *Chœropotamus* and thus may be considered as probably a member of the Chœropotamidæ, and moreover, there is additional evidence to show that this new genus is also closely related to *Parahyus* and *Helohyus*, also probably members of the Chœropotamidæ.

3. Cebochœridæ

Turning now to a comparison of *Brachyhyops* with *Cebochœrus* we see that points 3, 4, 5, 6, 7 and 9 listed as resemblances between *Brachyhyops* and *Chœropotamus* also hold as characters linking it with *Cebochœrus*. In addition certain other characters also serve as points of resemblance between these genera; for instance *Cebochœrus* has a short, broad skull as is the case with *Brachyhyops*. There are many differences, however, that serve to separate these genera. Of these may be mentioned points 3 and 4 cited as separating *Brachyhyops* from *Chœropotamus*, and in addition the following:

1. Size. *Brachyhyops* is much larger than *Cebochœrus*.
2. The vertical expansion of the zygomatic arches below the orbits.
3. The general shape of the preorbital portion of the skull.
4. The shape and structure of the cheek teeth.
5. The normal first premolars; these are caniniform in *Cebochœrus*.

It would seem that the differences separating *Brachyhyops* from *Cebochœrus* are greater than those separating it from *Chœropotamus*, as

[2]Matthew, W. D., 1909, Bull. 361, U. S. Geol. Survey, p. 95.
[3]Matthew, W. D. 1925, Amer. Mus. Novitates, No. 198, pp. 7-8.

might be expected, since both of the former genera show various specializations along separate lines of adaptive radiation.

4. Entelodontidæ

Achænodontinæ

Brachyhyops is like *Achænodon* in the following particulars:

1. The outlines of the cheek teeth.
2. To some extent in the great lateral expansion of the zygomatic arches.
3. The position of the orbit above the second and third molars.
4. To some extent in the shape of the glenoid; that is, in its shallowness and the transversely broad postglenoid process.
5. The position of the glenoid on a horizontal line with the occlusal surface of the teeth.
6. The position of the infraorbital foramen above the third premolar.
7. The closed dental series.

In certain respects, however, there are decided differences between the two genera. *Brachyhyops* differs from *Achænodon* in the following ways:

1. In its small size. Linearly the skull of *Brachyhyops* is less than half as large as the skull of *Achænodon*.
2. The anterior lateral expansion of the zygomatic arches.
3. The deep vertical expansion of the jugal beneath the orbit.
4. The closed orbit.
5. To some extent in the shape of the glenoid; that is in its extreme flatness and its antero-external boundary merging with the under surface of the zygoma.
6. The shape of the occiput. The difference here is partly a result of the great size in *Achænodon*.
7. The development of the separate parietal crests.
8. The rugose sculpture on the roof of the cranium.
9. The relatively shorter muzzle.
10 The presence of a first premolar.

Most of the resemblances outlined above are due to basic heritage characters that are common in many of the primitive bunodont artiodactyls. Some of them, such as the outlines of the cheek teeth and the shape of the glenoid, might be regarded as showing certain relationships between the two genera. On the other hand, there are many differences between *Brachyhyops* and *Achænodon*, differences that are clearly indicative of divergent specializations along separated

lines of adaptive radiation. Thus it would seem evident that any relationship established between these two genera must needs be carried back through their separate phylogenetic lines to their less specialized and therefore more closely related ancestors. *Brachyhyops* is seemingly a chœropotamid that has developed certain highly specialized characters—a point that was stressed in certain preceding paragraphs of this paper. *Achœnodon* on the other hand, approaches closely the true entelodonts of the Oligocene.

Entelodontinæ

In comparing *Brachyhyops* with the Oligocene entelodonts, resemblances are to be found in the closed orbits, the expansion of the jugal beneath the orbit, the low, transverse glenoid and the location of the infraorbital foramen above the third premolar. The first two of the above mentioned characters, namely the closed orbits and the expansion of the jugal beneath the orbit, are very probably parallelisms and thus are not indications of relationships between the genera. The other resemblances do not form a very strong link between *Brachyhyops* and the entelodonts. There are so many differences between *Brachyhyops* and the entelodonts that there is little doubt but that they are phylogenetically distinctly removed from each other. Among the characters whereby the entelodonts differ from this new genus may be mentioned the great size, elongation of the face and consequently of the teeth, the entirely different structure of the teeth, the position of the orbit back of the molars and its forward direction, the configuration of the cranium and the occiput, and finally the arrangement of the basicranium.

Of course these enumerated differences are all advanced habitus characters of the entelodonts, and it is quite conceivable that they may be secondary specializations from a *Brachyhyops*-like ancestral form. However, since *Brachyhyops* is contemporaneous with *Achœnodon* (a genus closely related to the entelodonts) and also with *Chœropotamus*, and since it is more nearly comparable to the latter than to the former of these two genera, it would seem reasonable to suppose that this new Uinta genus is of chœropotamid rather than of entelodont relationships. Naturally, because of its many primitive bunodont heritage characters, *Brachyhyops* is probably fairly close to the ancestor of the achænodonts and the entelodonts.

5. Tayassuidæ, Anthracotheriidæ, Agriochœridæ

Now there comes the question of certain more modern or advanced groups that might conceivably show resemblances to *Brachyhyops*. The most primitive pigs and peccaries indicate a mode of development that is quite out of line with the general *Brachyhyops* habitus. In the primitive pigs-peccaries the tendency is towards elongation of the muzzle and of the cheek teeth with consequent changes in the form of the whole skull. The Agriochœridæ and the Anthracotheriidæ are buno-selenodont artiodactyls, which it seems certain that *Brachyhyops* is not. In some of the agriochœrids there is a closing of the orbit and an expansion of the zygomatic arches, but any resemblances to *Brachyhyops* are very obviously due to convergence.

In the anthracotheres the tendencies are towards elongation of the face but not of the teeth, and the retention (except in the most advanced genera) of a rather primitive skull form. The probability that the Anthracotheriidæ are descended from a chœropotamid may account for any basic resemblances that exist between *Brachyhyops* and the anthracotheres.

Relationships of Brachyhyops

From the description and the comparisons set forth in the preceding pages of this paper, it becomes evident that *Brachyhyops* is an upper Eocene bunodont artiodactyl quite distinct from any of the genera of Bunodonta heretofore known to us. It would seem probable, however, that this new genus is a somewhat aberrant chœropotamid, possibly descended from *Parahyus* of the middle Eocene. Its assignment to the Chœropotamidæ must be regarded as somewhat provisional. *Parahyus* is here regarded as being more probably related to the Chœropotamidæ than to the Achænodontinæ.

In many of its characters *Brachyhyops* shows primitive heritage features common to numerous bunodont artiodactyls of the lower and middle Eocene of North America and Europe. But in size, the form of the teeth, the position and shape of the glenoid and the characters of the basicranium there would seem to be definite chœropotamid relationships. Certain skull characters are more or less similar to the corresponding characters in the entelodonts, particularly to the genus *Achænodon*, but numerous specializations in the skulls of both *Brachyhyops* and *Achænodon* would indicate that those genera have diverged greatly from their mutually related Middle or Lower Eocene ancestors.

Notes on the Relationships of the Bunodont Artiodactyls

The primitive bunodont artiodactyls have for many years caused a great deal of confusion to students who would attempt a classification of them. The various views as to their relationships have been exceedingly diverse, so that these early artiodactyls have been gathered together or split apart in all manners of combinations. Perhaps it may be well at this point to consider briefly a few of the most outstanding systems of artiodactyl classifications, with particular reference to the "bunodont" forms, in order that there may be an understanding of the basis for the use of the family and subfamily names appearing in the accompanying discussions.

In 1910 there appeared two comprehensive classifications of the Artiodactyla, namely, that of Osborn in his "Age of Mammals" and that of Stehlin in his great monograph on the Eocene mammals of Switzerland. Osborn grouped the primitive bunodont artiodactyls under one division which he called "Primitive Artiodactyls"—obviously an unnatural group. He subdivided the "Primitive Artiodactyls" into the "Bunodont Families," the "Bunoselenodont Families," and the "Selenodont Families." This classification included the Trigonolestidæ, Leptochœridæ and Dichobunidæ under the Bunodont group—a fairly satisfactory association. The Anthracotheriidæ constituted the Bunoselenodont group and the Anoplotheriidæ the Selenodont group. The Entelodontidæ, however, were separated from the other primitive artiodactyls and placed in the "Suina" together with the pigs, peccaries and hippopotami, where certainly they do not belong. Moreover there was a separate division of "Oreodonta" quite distinct from the anthracotheres and anoplotheres, to which the oreodonts are related.

Stehlin's classification, based mainly on characters of the teeth, demonstrates the faults of any classificatory system having so restricted a foundation. There are three great divisions of the artiodactyls, the Hypoconifera containing the two families, Dichobunidæ and Elotheriidæ, the Cainotheridæ and finally the Euartiodactyla comprising all of the remaining artiodactyls families. Naturally in this classification the bunodonts are divided between the Hypoconifera and the Euartiodactyla, all in all a somewhat inconvenient arrangement.

Since it has some bearing on the discussions presented on other

pages of this paper, there might be mentioned Depéret's monograph of 1917 on the Ludian fauna, in which *Chœropotamus* and *Cebochœrus* are included in the "Famille des Hyotherides."

In the 1925 revision of Zittel's "Text-Book of Palæontology" the artiodactyls are divided in part as follows:

Tribe 1. Bunodontia
Family 1. Suidæ Family 2. Leptocohœridæ
Family 3. Hippopotamidæ

Tribe 2. Bunoselenodontia
Family 1. Anthracotheriidæ Family 2.
Anoplotheriidæ Family 3. Dichobunidæ

Here the Dichobunidæ are separated from the Leptochœridæ, yet these two families are certainly closely related to each other. Another fault of this classification is that some of its "families" are too inclusive; thus the entelodonts and the peccaries are included in the Suidæ.

In 1927 Miss Pearson, using the basicranial characters as indices to taxonomic relationships, made a twofold division of the artiodactyls. In one of her groups the "Amastoid Artiodactyla," were included the Chœropotamidæ, Cebochœridæ, Anthracotheriidæ, Mixtotherium, Entelodontidæ, Hippopotamidæ and Suidæ. In the other group, the "Mastoid Artiodactyla," were placed the Dichobunidæ, Anoplotheriidæ, Cænotheriidæ, Agriochœridæ, Oreodontidæ, Tylopoda, Pecora and *Dacrytherium*, *Tapirulus*, and *Amphimeryx*. As in the case of Stehlin's classification, this arrangement suffers by being based on a single character.

In 1929 Dr. Matthew divided the Artiodactyla into five suborders, namely the Palæodonta, Hyodonta, Ancodonta, Tylopoda and Pecora. In the Palæodonta were placed the Dichobunidæ and the Entelodontidæ, while the Hyodonta consisted of the Tayassuidæ, Suidæ and Hippopotamidæ. This classification is probably the most logical of any of the systems so far considered, and it represents the results of many years devoted to the study of fossil and recent ungulates. Unfortunately Dr. Matthew never elaborated his classification.

His arrangement was followed by Simpson in 1931, but this latter author reduced Matthew's suborders Palæodonta and Hyodonta to superfamily rank, making them the Dichobunoidea and the Suoidea

respectively, and included them in a single suborder, the Bunodonta. He also placed the Leptochœridæ in the "Artiodactyla inc. sed."

In the recent textbook, "Vertebrate Palæontology," by Dr. A. S. Romer, the Artiodactyla are divided into two suborders; the Ruminantia in which the mastoid is exposed and the Suina in which the mastoid is excluded from the outer surface of the skull. It is at once evident that this classification follows the "mastoid" and "amastoid" divisions of the order, proposed by Miss Pearson. This arrangement, while theoretically sound, is practically inconvenient since it is based on a single character, which important as it may be, should not be allowed to overshadow the totality of diagnostic characters. Thus, in some of the primitive forms the division on the basis of the mastoid bone ignores very strong and undoubtedly important resemblances in the other skull elements, in the dentition and in the skeleton.

Scott's classification of 1913 and Hay's of 1930 are not considered in this discussion, since they are restricted to mammals of the Western Hemisphere and of North America respectively.

It is difficult to choose between Matthew's separation of the bunodont artiodactyls into two suborders, the Palæodonta and Hyodonta, and Simpson's inclusion of them in one suborder, the Bunodonta. In favor of Matthew's arrangement is the fact that it separates the essentially primitive, extinct bunodonts from the specialized, persistent forms. On the other hand, Simpson's arrangement places all of the bunodont forms together, so that they are set off as a group against the ancodont artiodactyls. Perhaps Matthew's arrangement is somewhat the better of the two, since it does recognize the distinction between the primitive and the advanced types.

Whatever arrangement of suborders is used, it seems to me that when superfamilies are considered, the dichobunids and the entelodonts are logically separable. In other words, these two groups deserve more than family distinction, accorded them in Matthew's and Simpson's classifications. Thus on the basis of subordinal and superfamilial relationships, the bunodont artiodactyls might be divided as follows:

Order Artiodactyla
1. Suborder Palæodonta
   a. Superfamily Dichobunoidea
   b. Superfamily Entelodontoidea

2. Suborder Hyodonta
   a. Superfamily Suoidea
   b. Superfamily Hippopotamoidea*

The basis for the above division of the Palæondonta may be presented in the following form:

Order ARTIODACTYLA

Suborder PALÆODONTA

Superfamily Dichobunoidea

Small, primitive artiodactyls. Skull usually of generalized form; certain specializations appear in the most advanced and latest genera. Basicranial foramina separate, basicranium normal, paroccipital processes short and projected posteriorly, auditory bulla usually cartilaginous. Orbit centrally located. Complete dental formula; upper molars with five or six cusps (protoconule and hypocone). Feet tetradactyl, metapodials not coalesced.

Superfamily Entelodontoidea

Large, specialized bunodont artiodactyls. Skull greatly modified, even in the most primitive genera. Basicranium compressed and foramina more or less coalesced, paroccipital processes short but massive, auditory bulla developed. Orbit usually displaced towards the posterior portion of the skull. Dental formula either complete or reduced; molars, upper and lower, four-cusped and elongated. Feet didactyl, but with the metapodials not coalesced.

This twofold division of the Palæodonta would seem to be a more or less natural one, whereby the small, primitive and ancestral types are separated from the large, specialized forms. In this connection it might be pointed out that the ancestral dichobunids first appear in the lower Eocene and persist on to the top of the Eocene, whereas the derivative entelodonts do not appear until the upper Eocene and develop to the height of their evolutionary expression in upper Oligocene and lower Miocene times.

Various families and subfamilies may be created to include the genera belonging to the Dichobunoidea, according, for the most part, to the individual preference of the author. The arrangement given

*In my opinion the Hippopotamuses probably belong to the Ancodonta, as descendants of the Anthracotheres, rather than to the Hyodonta, as descendants of the Pigs. See Colbert, E. H., 1935, Amer. Mus. Novitates, no. 799, pp. 10-23; also Trans. Amer. Phil. Soc., N. S., XXVI, pp. 288-294.

below is presented here as the basis on which the comparisons of various genera have been made in other pages of the present paper.

a. Superfamily Dichobunoidea
   - a[1]. Family Dichobunidæ Turner, 1849.
   - b[1]. Family Chœropotamidæ Owen, 1840-5.
   - c[1]. Family Cebochœridæ Lydekker, 1883.
   - d[1] Family Leptochœridæ Marsh, 1884.

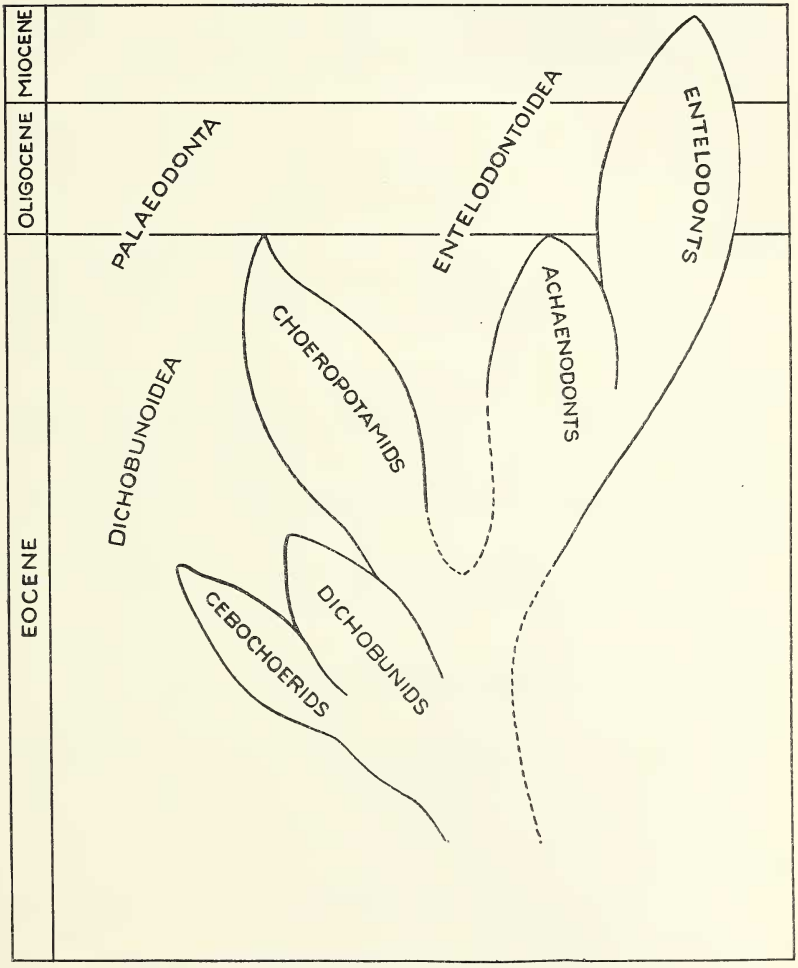

FIG. 5. Phylogeny of the bunodont artiodactyls.

This classification is anything but perfect, and is offered merely as a background for the collateral discussions that have to do with the relationships of *Brachyhyops*. Various possibilities immediately suggest themselves in regard to the above arrangement of the Dichobunoidea. For instance, it might be preferable to divide both the Dichobunidæ and the Chœropotamidæ into several families. On the other hand, the Cebochœridæ might be included in the Chœropotamidæ, while the Leptochœridæ might be placed under the Dichobunidæ. Then again, the Leptochœridæ may properly be excluded from the Dichobunoidea, as was done by Simpson in 1931.

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*Since this paper was submitted for publication, the new edition of Professor Scott's "History of Land Mammals in the Western Hemisphere" has been issued. On page 393 of his work, Professor Scott notes the resemblances and differences between *Brachyhyops* and the entelodonts (in which group he includes *Achænodon* and *Parahyus*). He includes *Brachyhyops* provisionally in the "entelodont family."